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Changes in feeding attributes of four collembolan populations during the decomposition process of pine needles

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Summary. Changes in population abundances of four collembolan species during decomposition processes of pine needle litter were studied using a litter bag method over a two year period in a pine forest. The resource conditions of decomposing litter were expressed by the C/N ratio and fungal abundances on/in needle litter. The two surface-dwelling species (*Tomocerus varius* and *Lepidocyrtus lignorum*) predominated in the early decomposition stages, while the two humus-dwelling species (*Folsomia octoculata* and *Onychiurus flavescens*) (increased their abundances with the advance of decomposition. The gut content analysis of the four species showed that gut contents consisted mainly of plant and fungal materials. *F. octoculata* and *T. varius* showed a switching of feeding depending upon food availability during decomposition. While *L. lignorum* and *O. flavescens* showed no switching of feeding and were fungal and detritus feeders respectively. The abundances of *T. varius* and *L. lignorum* were positively correlated with the C/N ratio and were high in the fungal growing state, i.e. immobilization stages. The abundances of *O. flavescens* and *F. octoculata* were negatively correlated with C/N ration of litter during its decomposition. The joint study of collembolan populations and food resources showed two feeding strategies, i.e., the specialist (*O. flavescens*, and *L. lignorum*) and generalist (*F. octoculata* and *T. varius*) feeding and the changes in population abundances of these species were explained by their feeding attributes.

Key words: Collembola, fungal abundance, feeding habit, gut contents, C/N ratio, decomposition

1. Introduction

Decomposition processes occur as a result of interactions between the physical and chemical properties of litter and its microbial and soil animal populations (Swift et al. 1979). In the soil system, plant litter is a main resource for the organization of soil organisms and is changed through the interactions between microbial and animal decomposers. Decomposing litter provides both the food and habitat resources for soil organisms (Takeda 1994).
Faunal succession during decomposition processes has been demonstrated in a number of soil animals such as Acari and Collembola (e.g., Anderson 1975; Hågvar & Kjøndal 1981; Takeda 1987) and study of feeding attributes of soil animals is important for an understanding of their successional changes during the decomposition processes. Collembola and Cryptostigmata are detritivorous or fungivorous in their feeding habits (Luxton 1972; Petersen & Luxton 1982), and exploit food resources such as fungi and plant debris provided during decomposition processes of litter. Changes in feeding attributes of soil animals have been demonstrated for Collembola (Hågvar & Kjøndal 1981) and Cryptostigmata (Anderson 1975), but were not related to food availability during the decomposition processes of litter.

Joint studies of soil animal populations and resource dynamics of decomposing litter are important for the interpretation of successional patterns of soil animals, since these changes are responses of species to the availability of food resources during decomposition processes.

The objectives of the present study are to interpret the successional changes of Collembola through the analysis of their feeding attributes during the decomposition processes of pine needle litter in a pine forest. A further aim of this study is to assess the roles of collembolan species in decomposition processes.

Materials and Methods

Study area

The study was carried out in a natural forest of Japanese red pine (*Pinus densifolra* Sieb. et Zucc) mixed with *Chamaecyparis obtusa* Endle at Kamigamo Experimental Forest Station of Kyoto University, about 12 km north of Kyoto city (35° 04′ N and 135° 43′ E): Details of the study area have been reported in Takeda (1976, 1978). A study plot of 10 m × 10 m in area was laid out in the pine forest. Meteorological records were obtained from the station. Mean annual precipitation and evaporation were 1,678 mm and 985 mm respectively. The surface litter layer often dries out in May and mid summer. The soil humus form in this study area was a Moder with a poorly developed mineral soil horizon (A) which is about 1 cm in thickness. The A_0 layer consists of L, F and H layers, ranging from 2 to 5 cm in thickness. The transition between the H and A layers is indistinct, but the boundary between the A and B layers is very sharp. The A_0 layer is the main habitat for the soil microarthropods in this study area (Takeda 1976).

Litter bag methods

Decomposition processes of pine needle litter were studied by a litter bag method (Crossley & Hoglund 1962). Newly fallen needles of *Pinus densiflora* trees were collected from the forest floor in December 1989. Litter bags (each 10 cm × 10 cm in area with a mesh size of 3 mm) were used for the decomposition study. Three grams of air-dried pine needles were placed in each litter bag. This litter mass approximated the litter falls in this study area (Takeda 1988). The litter bags were set out in a 10 m × 10 m study plot divided into 10 sub-plots each 2 m × 5 m in area. A 1 m × 1 m area was laid out in each subplot to contain 20 litter bags. Litter bags were placed on February 29, 1990. After the removal of newly fallen litter, the litter bags were fastened to the forest floor by metal pins to prevent movement and to ensure a good contact between the litter bags and the organic layers.

Litter bags were collected every 3 months from May 1990 to February 1992. On each sampling occasion, 20 litter bags were collected from the study plot (i.e. 2 litter bags were collected from each sub-plot), returned to the laboratory, and used for the study of soil animal populations, fungal colonization, and chemical analysis of litter.

Chemical analysis of needle litter

After the extraction of soil animals, samples of litter were used for chemical analysis. Samples of initial and decomposing needles were dried at 80 °C to a constant weight and ground in a laboratory mill to pass a 0.5 mm screen. Total nitrogen and carbon of pine needles were measured by automatic gas chromatography (C-N corder, Yanagimoto Co., Japan). The decomposition rate of needle litter was estimated using the expontential decay model of Olson (1963); $DM/DM_0 = \exp(-kt)$ (where k is the decay constant, t is the year, DM_0 = original mass of dry matter, DM = mass of dry matter after a given period).

Nitrogen and carbon contents of litter after a given period of decomposition were calculated by the following formula; Remaining mass (percentage) = $C/C_0 \times DM/DM_0 \times 100$, (where C_0 = inital concentration of N or C in litter and C = concentration of nitrogen or carbon after a given period).

Estimation of hyphal lenghts

Fungal abundances were estimated during the decomposition processes of needle litter over a 24 month period. On each sampling occasion, 10 of the 20 litter bags collected were used for the estimation of fungal abundances after extraction of the soil animals. In this study both the hyphal lengths on the surface and within the pine needles were estimated. The hyphal lengths on the surface of needle litter were estimated at 3 monthly intervals during the study period, whereas hyphal lengths within the needle litter were estimated on four occasions, i.e. May and November in 1990 and 1991.

To estimate the hyphal lengths both on and in the needle litter, one gram of pine needles was boiled with distilled water for an hour. Then the surfaces of needles were rinsed by an ultrasonic washer to ensure the collection of fungi from the needle surfaces. The rinsed needles were used for the estimation of fungi colonizing in the needles and the rinse water was used for the estimation of fungi colonizing the needle surfaces.

After the rinsing of needles, the rinse water was diluted to 400 cc with distilled water, and further diluted by transferring 100 ml into 300 ml distilled water twice (dilution 16-1). Dispersing the dilution by an electric stirrer, 2 ml of the suspension were pipetted onto a Millipore filter holder containing a membrane filter (MF-Millipore filter 0.8 μm pore size with 47 mm diameter, Millipore Co) (Hanssen et al. 1974). Then, 100 ml of distilled water and 2 ml of fuchsin stain with lactic acid were added. After the staining process of 3 minutes, the stained suspensions was drawn through the filter using vacuum suction. After the filtration, the Millipore membrane filter was dried and transferred to a glass microscope slide. The filter was covered with immersion oil (Nikon, clearing agent) and a coverslip was placed over the surface. One membrane filter slide was prepared for each litter bag sample. Hyphal lengths were measured using a microscope with a 10×10 grid eyepiece graticule at a magnification of $400 \times$. Hyphae of forty fields of view were counted per sample and hyphae were traced on a paper using a microscope ($400 \times$) with drawing apparatus (Nikon).

After the collection of surface fungi, the needles were homogenized in 200 ml water with an electric ultra-homogenizer run at 3000 rpm for 3 min and homogenate was used for the estimation of fungi within the needles. Measurement of hyphal lengths in the needles was carried out as in the case of surface fungal hyphae measurements. Morphological changes in needle litter were studied using a scanning electron microscope and optical microscope. These studies were qualitative, designed to provide a visual record of microbial colonization on/in needles and animal feeding scars on needles during the decomposition process.

Collembolan populations and gut content analysis

Changes in soil animal populations were studied by litter bag methods. On each sampling occasion, twenty litter bag samples were collected and were used for the estimation of collembolan populations. Soil animals in the litter bags were extracted by a modified Tullgren funnel at a constant temperature conditions of 35 °C in a cabinet for 3 days. Animals were collected in 99% ethanol. Identification, counting and measurements of soil animals were carried out under a binocular microscope with a magnification of $400 \times$.

In this study plot, soil fauna was dominated by microarthropods such as Collembola and Acari. The life cycles and population dynamics of collembolan species have been studied at this site by Takeda (1976, 1979, 1984, 1987). In this plot, the collembolan community consists of 36 species and collembolan species were divided into feeding groups, i.e. 5 suctorial and 31 detritivore species, on the basis of mouth-part morphology. The detritivore species were dominant in the collembolan community in terms of population abundance and species numbers (Takeda & Ichimura 1983). In this study, four detritivorous species were selected for the gut content analysis. Two species, *Folsomia octoculata* and *Onychiurus flavescens*, were humus-dwelling species. The other two species, *Tomocerus varius* and *Lepidocyrtus lignorum*, were surface-dwelling species (Takeda 1979).

The specimens of the four species were sorted from samples and preserved in lactic acid for one week. For each species, the number of individuals with gut contents was counted. The specimens with visible gut contents could then be selected for further analysis. On each sampling occasion, thirty fed individuals were selected from each species. They were divided into three sub-samples containing 10 individuals and their gut contents were combined for analysis. The gut contents of 10 individuals were mounted in a small drop of glycerol on a glass slide and dispersed by lightly pressing the cover slip.

Seven categories of foods were classified as follows; plant material, fungal hyphae, fungal spores, pollen, mineral particles, algae and animal remains. Gut contents were examined with a binocular microscope of $400 \times$ magnification. The area of each food particle was measured by a microscope

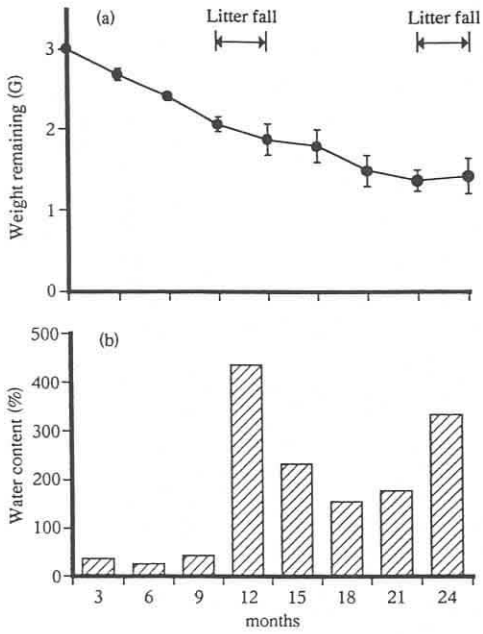

Fig. 1. (a) Mean weight of needles in litter bags during the decomposition process. (Bars indicate standard errors.) (b) Changes of water content of litter

with a gridded eyepiece having a total of 100 squares. Five replicates of (i.e. 500 squares) views were examined for each gut sample. The percentage of each food was calculated on the basis of their relative areas.

Results

Change in the litter mass and water content during decomposition

Changes in weights of pine litter were followed over a 2 year period from March 1991 to October 1993 and are shown in Fig. 1 (a). Decomposition rates of pine needles were expressed using the decomposition constant of Olson (1963) and were $k_1 = 0.039\ \text{month}^{-1}$ for the first year and $k_2 = 0.023\ \text{month}^{-1}$ for the second year respectively. The decomposition rates decreased with the field exposed time and were significantly higher in the first than in the second year.

Changes in water contents of pine litter were monitored over 24 months and are shown in Fig. 1 (b). In the first 9 months, water contents ranged from 50 to 60%. Water contents of needle litter increased sharply after the end of the litter fall period in winter. Then, water contents of litter ranged from 150–450% through the rest of study period. High humidity conditions of pine litter were maintained during the second year by the coverage of newly fallen litter on the litter bags.

Carbon and nitrogen dynamics of needle litter

Changes in carbon mass were similar to those in pine needle weight loss (Fig. 2 (a)). While, the changes in nitrogen mass showed three phases; (1): leaching loss in the first 3 months, (2): initial net immobilization during 3 to 9 months, and (3): steady-state during 9–24 months (Fig. 2 (b)). Nitrogen mass decreased by about 7% of the original amounts during the first leaching phase. Then, nitrogen mass increased to 145% of the original mass during the initial net immobilization phase. Finally the nitrogen mass was in steady-state over the rest

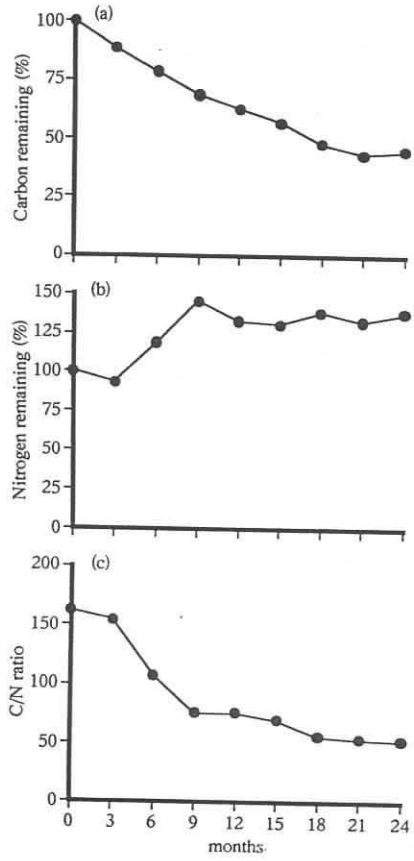

Fig. 2. Carbon and Nitrogen dynamics in litter. (a) Carbon amount, (b) Nitrogen amount, (c) C/N ratio

of the study period. Fig. 2 (c) shows the C/N ratios during the decomposition period. The C/N ratio was 162 for the initial needle litter, then decreased to 154 during the leaching phase from 0 to 3 months. During the net immobilization phase from 3 to 9 months, the C/N ratio changed from 154 to 76. Then, the C/N ratio changed gradually from 76 to 56 during 9 to 18 months. The C/N ratio reached a critical level of about 55 and was then stable during the rest of the study period. Changes in resource quality of litter took place mainly during the net immobilization phase from 3 to 18 months after the placement of litter bags.

Colonization processes of fungi on and in the needles

Fig.3 (a) shows the changes in hyphal lengths on the needle surface during decomposition processes. Fungal colonization both on the litter surface and within litter were monitored over 2 years. Hyphal lengths on the litter surface increased from 165 m/g litter to 3100 m/g litter during 3 to 18 months, and then decreased to 2060 m/g litter at 24 months during the rest of the study period. Patterns of fungal colonization on the needle surfaces were characterized by three phases as follows; 1. phase 1: growth (3 to 9 months), 2. phase 2: steady-state (12 to 18 months), and 3. phase 3: collapse (21 to 24 months). During phases 1 and 2, fungal growth on needle surfaces was well represented by a logistic equation. During phases 1 to 3, hyphal lengths on the needle surface were significantly related to the C/N ratio ($p < 0.01$, $r = -0.935$, d.f. $= 4$), suggesting the immobilization of nitrogen by fungal growths on the pine needles.

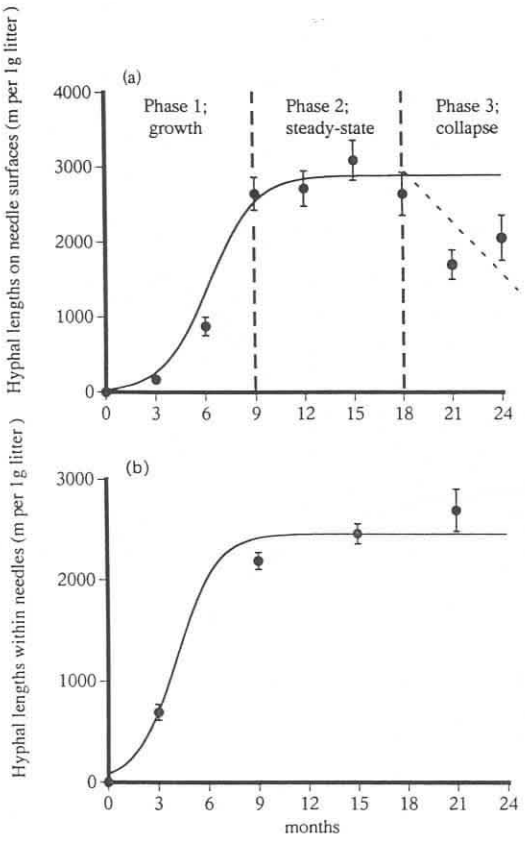

Fig. 3. (a) Lengths of hyphae colonizing needle surfaces. A solid line was calculated on the data from months 0–18. The formula of this line is $Y = 2900/(1 + 87 \times \exp(-0.7 \times X))$ where X = months after the experiment has started, Y = hyphal lengths (m), $R^2 = 0.97$. The dotted line after 18 months is drawn freehand. Bars indicate standard errors. (b) Lengths of hyphae colonizing within needles. The formula of this line is $Y = 2500/(1 + 30 \times \exp(-0.8 \times X))$ where X = months after the experiment has started, Y = hyphal lengths (m), $R^2 = 0.98$. Bars indicate standard errors

Fig. 3 (b) shows the changes in hyphal lenghts in the pine needles. Hyphal lengths in the needle increased from 693 m/g litter to 2694 m/g during 3 months to 21 months. Fungal length increased rapidly during the period from 0 to 9 months as in the case of the surface fungi, then the rates decreased during the rest of the study period.

Observations by SEM revealed the processes occurring on/in the pine needles during the decomposition. Needles remained intact during the leaching and immobilization phase, but with the advance of decomposition the surface of needles were colonized by fungi (Fig. 4). These fungi colonized the wax and epidermis layers of needles during the immobilization phase. After one year, the surfaces of needles were completely covered by the fungal mycelium, and the wax and epidermis were converted into fungal biomass.

Changes in soil animal populations during the decomposition

Relative abundances of soil animal groups in the litter bags are shown in Table 1. Collembola and Cryptostigmata were predominant groups in the litter bag fauna and each accounted for 33% and 30% of the total animal abundances respectively. The relative abundances of collembolan populations in the litter bags are shown in Table 2. Collembolan communities consisted of 31 species. The relative abundances of the four species selected for gut contents analysis were as follows; *Folsomia octoculata* (36%), *Tomocerus varius* (13%), *Onychiurus flavescens* (11%), and *Lepidocyrtus lignorum* (7%).

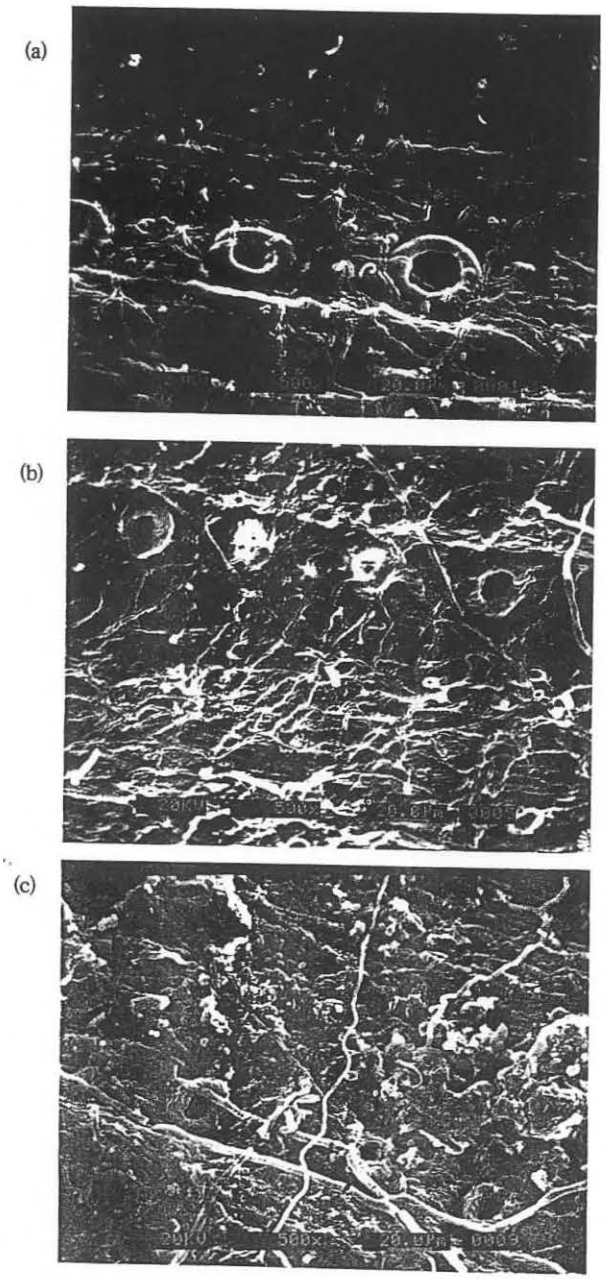

Fig. 4. Morphological changes on the surfaces of needles in the litterbags using a scanning electron microscope (SEM) during the decomposition process. (a) Surface of needle at the 3rd month. (b) Surface of needle at the 12th month. (c) Surface of needle at the 24th month

Table 1. Relative abundances of soil animals colonizing the litter bags during the study period

Group	Population density (m^{-2})	Relative abundance (%)
Collembola	4176.3	33.214
Cryptostigmata	3801-3	30.232
Mesostigmata	1438.8	11.443
Astigmata	1438.8	11.443
Prostigmata	1002.5	7.973
Diptera	324.4	2.58
Thysanoptera	141.3	1.123
Enchytraïdae	113.8	0.905
Isoptera	73.7	0.586
Diplopoda	21.9	0.174
Coccoidea	6.9	0.055
Coleoptera	5.6	0.044
Lepidoptera	5.6	0.044
Araneae	4.4	0.035
Amphipoda	4.4	0.035
Pseudoscorpiones	3.7	0.029
Pauropoda	2.5	0.02
Protura	1.9	0.015
Opiliones	1.2	0.01
Hymenoptera	1.2	0.01
Chilopoda	1.2	0.01
Symphyla	1.2	0.01
Isopoda	0.6	0.005
Haprotaxida	0.6	0.005
Total individuals	12573.8	

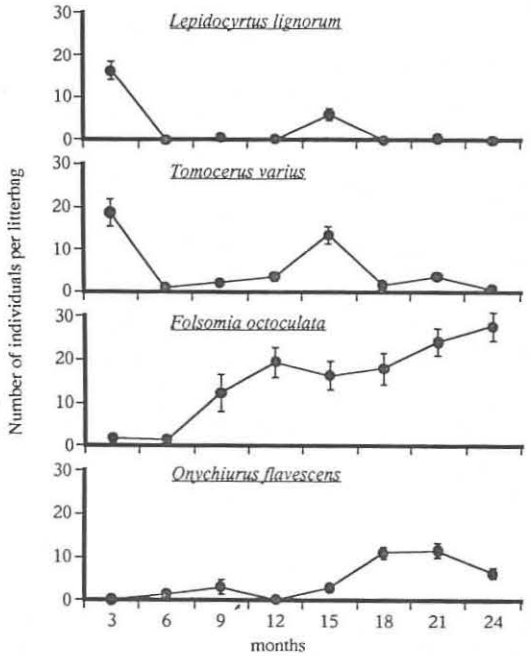

Fig. 5. Changes in numbers of four species of Collembola . Bars indicate standard errors

Table 2. Population density of Collembola colonizing the litter bags during the study period

Species name	Population density (m^{-2})	Standard errors
Folsomia octoculata	1513	128
Tetracanthella sylvatica	607	109
Tomocerus varius	552	71
Onychiurus flavescens	457	52
Lepidocyrtus lignorum	289	53
Xenylla humicola	206	36
Odontella sp.	142	30
Isotoma sensibilis	135	20
Homidia subcingula	71	11
Megalothorax minitus	40	9
Tullbergia yosii	25	5
Oncopodura crassicornis	21	5
Sminthurus sp.	18	4
Sminthrinus sp.	18	6
Isotoma carpenteri	13	5
Entomobrya sp. 1	11	4
Homidia sp.	10	3
Friesea sp.	9	5
Micranurida sp.	6	5
Lepidocyrtus sp. 2	6	3
Tomocerus punctatus	6	2
Lophognathella choreutes	6	2
Neanura mandarina	4	2
Neanura sanctisebastiani	4	2
Arrohopalites sp.	3	2
Entomobrya sp. 2	2	1
Dicyrtoma sp.	1	1
Isotomiella minor	1	1
Hypogastrura sp.	1	1
Total	4177	

Fig. 5 shows the changes in population abundances of the four species during the decomposition processes of litter. At the 3 month sampling, *T. varius* and *L. lignorum* were predominant and each accounted for 39% and 34% of the total collembolan abundance. The humus-dwelling species, *F. octoculata* and *O. flavescens*, increased their abundances during the immobilization phase of needle litter. After 18 months, abundances of the two species accounted for 69% of total collembolan abundance. While the two surface-dwelling species. *T. varius* and *L. lignorum*, decreased their abundances during the period from 18 to 24 months.

Changes in gut contents of selected Collembola species

In every species, gut contents consisted largely of plant and fungal materials and the other components constituted a minor proportion of their food (Table 3). Fig. 6 shows the variations in percentages of plant and fungal material in gut contents of the four species over a 2 year period. For each species, the variations of plant and fungal material during the decomposition process were examined using ANOVA. The proportion of plant and fungal materials in the guts of *T. varius* and *F. octoculata* showed a significant variation in

Table 3. Mean composition (relative proportions of components) of the gut contents of four species of Collembola during the experimental period

Food source	*T. varius*	*F. octoculata*	*O. flavescens*	*L. lignorum*
Plant material	64.5	76.7	81.9	47.2
Fungal hyphae	34.3	22.8	17.7	44.2
Fungal spores	0.5	0.3	0.2	8.5
Pollen	0.3	0.1	0.0	0.0
Mineral particles	0.2	0.1	0.1	0.1
Algae	0.1	0.0	0.1	0.0
Animal remains	0.1	0.0	0.0	0.0

gut contents over the study period ($P < 0.01$). Changes in feeding preferences of *T. varius* and *F. octoculata* were examined by the regression analysis between the decomposition time (month) and percentages of fungal materials in each species. The results are shown in Fig. 7. At the first sampling, the proportion of fungal materials in the gut contents of *T. varius* and *F. octoculata* were 45 and 30% respectively. Then the percentage of fungal material in gut contents of the two species decreased with the advance of decomposition stages. The

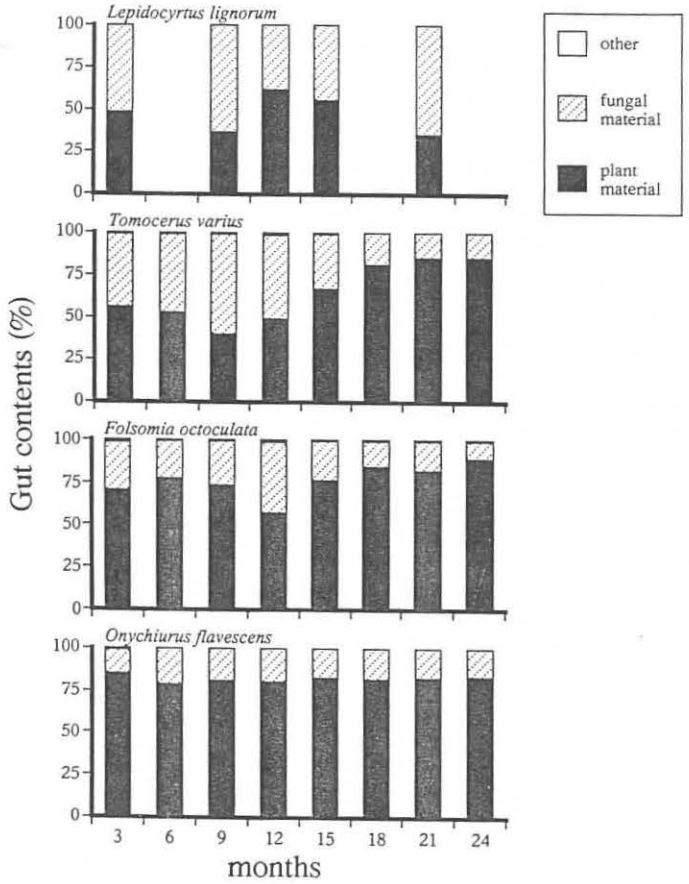

Fig. 6. Gut contents of four species of Collembola

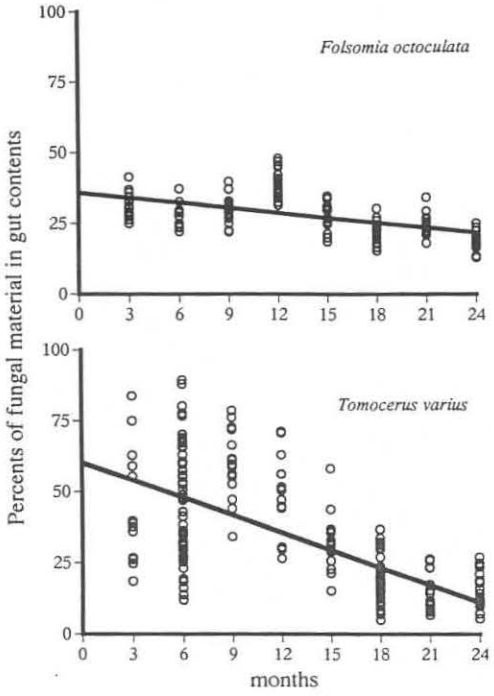

Fig. 7. Changes in percentage of fungal material in gut contents. Dots show the values for each sample. The formula of a solid lines are $Y = -0.538X + 35.9$. $R^2 = 0.285$ *(F. octoculata)* and $Y = -2.06X + 60.2$, $R^2 = 0.444$ *(T. varius)* where X = months after the experiment has started, Y = percentage of fungal material in gut contents

decomposition advanced. Switching of feeding from fungal to detritus materials were more pronounced in *T. varius* than in *F. octoculata.*

In the cases of *L. lignorum* and *O. flavescens*, there was no switching of feeding during the decomposition process. The overall mean proportions of fungal materials in the gut contents of *L. lignorum* and *O. flavescens* were 55 and 20% respectively and those of plant materials were 45 and 80% respectively. There were significant differences in the gut contents between the two species over the study period in that *L. lignorum* and *O. flavescens* specialized in fungal and detritus feeding respectively.

Relation between abundances of collembola species and litter quality

The relationships between the abundances of the four species and the litter quality were examined and the results are shown in Table 4. The food availability of litter was expressed by the abundances of fungi and litter quality shown by C/N ratio. Fungi is an important food item for collembolan species. Based on the abundance of fungi and the C/N ratio of litter, the decomposition of the pine needles is characterized by three phases.

Densities of *L. lignorum* were significantly high during phase 1, when fungal populations were in a growth phase. Densities of *T. varius* were significantly high during phases 1 and 2. *F. octoculata* and *O. flavescens* both increased their densities with the advance of decomposition over the study period.

The densities of *F. octoculata* were negatively correlated with the C/N ratios of needle litter ($p < 0.01$, $r = -0.873$; d.f. = 6). Weak negative correlation was found between C/N ratio and densities of *O. flavescens* ($r = -0.684$). While, the densities of *L. lignorum* were positively correlated with the C/N ratios ($p < 0.05$, $r = 0.802$). Weak positive correlation was found between C/N ratio and densities of *T. varius* ($r = 0.662$).

Table 4. Relation between abundances of Collembola species and litter quality

	Phase 1 (3 to 9 months)	Phase 2 (12 to 18 months)	Phase 3 (21 to 24 months)	
Resource quality				
Fungal abundances on needle surface (m/g)	1230 (165 – 2650)	2820 (2650 – 3100)	1880 (1700 – 2060)	
Fungal abundances in needles (m/g)	1440 (693 – 2187)	2457	2694	
C/N ratio	113 (76 – 155)	67 (56 – 76)	53 (53 – 56)	
Abundances of Collembola species (numbers/g of litter)				
Tomocerus varius	2.76 (0.37 – 6.94)	3.44 (1.00 – 7.44)	1.54 (0.45 – 2.62)	Phase 2 > *3
Folsomia octoculata	2.41 (0.60 – 5.97)	10.45 (9.06 – 11.97)	18.59 (17.59 – 19.60)	Phase 1 < **2 < *3
Onychiurus flavescens	0.70 (0.04 – 1.46)	3.02 (0.11 – 7.33)	6.48 (4.49 – 8.47)	Phase 1 < **2 < **3
Lepidocyrtus lignorum	1.90 (0 – 5.41)	1.00 (0 – 2.94)	0.12 (0 – 0.25)	Phase 1 > **3

Numbers above a parenthesis show mean values. Numbers in a parenthesis mean minimum (left) and maximum (right) values. * $P < 0.05$, ** $P < 0.01$

Discussion

The decomposition processes of pine needles were characterized by the litter quality and by the fungal and animal abundances (Table 4). In this study, the fungal colonization patterns were characterized by the three phases as follows: (1). growth phase during 3 to 9 months, (2). steady-state phase during 12 – 18 months, and (3). collapse phase during 21 to 24 months. The fungal abundances increased during the growth phase and fungal populations contributed to both the net immobilization of nitrogen and mineralization of carbon. The immobilized nitrogen was maintained during the steady state phase, while the carbon showed mineralization by the fungal metabolism. During the collapse phase, carbon and nitrogen of litter began to mobilize when the C/N ratio reached a critical level of 55. Staaf & Berg (1982) have interpreted the dynamics of carbon and nitrogen as a resource utilized by microbial populations and showed that a critical level of C/N was 60 in Scots pine needles. Fungal growth contributed greatly to the changes in carbon and nitrogen (and hence C/N ratio) during the decomposition process. The contributions of fungi to nitrogen and carbon dynamics have also been shown in a number of decomposition studies of leaf litter (Berg & Söderström 1979; Bååth & Söderström 1979; Ausmus et al. 1979).
During the decomposition process, such changes in litter quality are brought about by fungal growth which thus facilitates the colonization of Collembola. The changes in abundances of the four collembolan species and the gut contents of the Collembola were studied in conjunction with food availability during the decomposition phases. In the nutrient immobilization phase, fungal populations grew and *T. varius*, and *L. lignorum* were predominant. Analysis showed that *T. varius* and *L. lignorum* had higher proportions of fungal materials in their guts during this phase, suggesting that the two species grazed selectively on fungal material. Hågvar & Kjøndal (1981) showed that *L. lignorum* was a typical microphytophage, and was a pioneer species in the early decomposition stages of birch litter. The pioneer species have the strategy of a high mobility in the litter layer and a well-developed ability to identify their food items, such as fast-growing, spore-producing fungal colonies, in their microhabitat.

With decomposition proceeding, the C/N ratio became low and humus and animal feces increased in the steady state phase. In this phase, the abundances of *F. octoculata* and *O. flavescens* increased with the decomposition process and were significantly negatively related to the C/N ratio of needle litter. *O. flavescens* and *F. octoculata* continued to increase even after 24 months during the mobilization phase of needle litter (Takeda 1987). The two species had low proportions of fungal materials and the gut contents consisted of high proportions of plant material. The detritivorous Collembola can consume plant detritus partially digested by microbial populations. In this study the two fungivorous collembolan species were early colonizers, while the two detritivorous species were later colonizers in the decomposition. These changes in abundance were related to the feeding attributes of the species. Thus, the successional changes of the four collembolan species were explained by their feeding habits and were related to food availability at each decomposition phase.

The feeding habits of soil animals are many and varied (Petersen & Luxton 1982). However, here the joint study of collembolan populations and food resources revealed two feeding strategies, i.e. specialist and generalist feeding. *O. flavescens* and *L. lignorum* were specialist in their feeding habit, the former being plant debris feeding, the latter fungal feeding. The early colonizer, *L. lignorum*, was fungivorous and the pioneer species in the decomposition stages. The pioneer species are less abundant compared with species inhabiting the thick underlying organic layers because the microbial "flush" period is short and normally limited to a thin top litter layer. The other specialist, *O. flavescens*, depends upon the decomposing plant litter and its population density was high in the moder humus forms (Takeda 1987). *T. varius* and *F. octoculata* were generalists in their feeding habits, selecting food according to its availability in each of the decomposition stages. The proportions of fungal material in their guts decreased during litter decomposition when they switched from fungivore to detritivorous.

Such a switching of feeding habit was shown for some Cryptostigmata (Acari) species during the decomposition of leaf litter by Anderson (1975) and was attributed to increased palatability of plant materials after leaching of poly-phenols from leaf litter during decomposition. The ability of switch to their feeding habits allows collembolan species to exploit wider food niches. In this study area, *T. varius* and *F. octoculata* are each dominant surface and humus dwelling species respectively (Takeda 1979, 1987). The dominance of the two species may be explained by the switching ability in their feeding depending upon the availability of food items during the decomposition states in the organic soil layers. The generalist feeding of Collembola may also provide an explanation for the differences of feeding selection of collembolan species noted between the field and laboratory studies (Takeda & Ichimura 1983).

Collembola are detritivorous or fungivorous in their food utilization during the decomposition of litter and have a poor ability to comminute pine needle litter. Their roles in decomposition processes of needle litter may be indirect through their interaction with the fungal populations and may change during the decomposition process (Takeda 1994). In the initial decomposition stages, during which fungal populations were in a growth phase, the surface-dwelling species, *T. varius* and *L. lignorum* utilize the fungi colonizing the needle surfaces. The surface-dwelling species may be contributing to the immobilization process of fungi by eliminating the senescent hyphae through their grazing activities. The surface-dwelling species predominated in the L layer but their population may be variable depending upon environmental conditions such as humidity. The grazing Collembola may also be prevented from over-exploiting fungal populations by limitations imposed by predation pressures and environmental variability in the L layer. Thus, they might promote nitrogen immobilization rather than mobilization by fungal populations through their grazing activities.

During the immobilization of fungal populations, the needle litter was changes into fungal biomass (alive and senescent) and the grazing Collembola deposited their feces on the needle surfaces. The interaction between the grazing Collembola and fungal populations may increase food availability for the detritivorous collembola species. In the later decom-

position stages, the decomposition rates decreased, while the collembolan abundances usually increased (Takeda 1994, 1987). Anderson & Healey (1973) suggested that coprophagy might be expected to be a major industry among soil animals. Coprophagy is a sort of recycling utilization of resources and may increase food availability for the detritus feeder. The later colonizing species, *O. flavescens* and *F. octoculata*, may contribute to the recycling of organic matter through their coprophagy and detritus feeding. Decomposition processes of pine needles consisted of immobilization and mobilization phases. The specialist feeders contributed to either the grazing effects in the immobilization phase or the recycling process in the mobilization phase, while the generalist feeders contributed to both processes and were dominant in the Moder humus form in this study area.

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